The Influence of Climate on Phytoplankton Communities in the Upper San Francisco Estuary

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ABSTRACT: The 1977 climate shift was characterized by low chlorophyll *a* concentrations and a shift in phytoplankton community composition throughout the upper San Francisco Bay estuary. Average chlorophyll *a* concentration decreased by a factor of 2 and was associated with a loss of diatoms, particularly pennate diatoms, and an increase in flagellates. These changes in phytoplankton biomass and community composition reflected interannual variations in water-year types. Water-year types are a function of climate, which changed to very dry conditions after the 1977 climate shift. For climate to be a driving force in phytoplankton communities, it must affect mechanisms that control biomass and community composition. The influence of climate on environmental conditions and phytoplankton community composition among water-year types was examined using 19 years of physical, chemical, and phytoplankton data collected monthly at 15 stations throughout the estuary. Environmental variation associated with the ENSO climatic signal for different water-year types was isolated using covariance analysis and summarized using principal component axes. Correlations between the principal component axes describing climatically-related environmental variation and chlorophyll *a* concentration plus phytoplankton density and biovolume for individual species and species groups suggest dry conditions produced by the 1977 climate shift were at least partly responsible for the changes in phytoplankton biomass and community composition measured between 1975 and 1993.

Introduction

Average annual chlorophyll *a* concentration decreased by a factor of 2 for most regions in the upper San Francisco estuary after 1976 (Lehman 1996a, 1992). The lower chlorophyll *a* concentrations after 1976 were accompanied by a loss of diatoms and a shift in the composition of the phytoplankton community toward more greens, bluegreens, and flagellates (Lehman and Smith 1991; Lehman 1996a). Many factors can influence phytoplankton biomass such as management practices that affect downstream transport (Jassby and Powell 1994) and grazing by introduced clams (Nichols 1985). The role of toxic substances is unclear but suspected to be important for changes in biomass and community composition. Natural environmental change associated with the 1977 climate shift may also be important. That climate was important is suggested by coincident changes in chlorophyll *a* concentration, phytoplankton community composition, and environmental variables with the 1977 climate shift (Lehman and Smith 1991). Recent studies also suggest that chlorophyll *a* concentration and community composition vary with water-year type, which is directly related to the climate (Lehman 1996a).

The purpose of this study was to determine if climate-related changes in environmental conditions may have influenced the changes in phytoplankton community composition and biomass measured among

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water-year types between 1975 and 1993 in the upper San Francisco Bay estuary.

Methods

Environmental and biological variables were measured monthly or semimonthly at 15 stations between 1975 and 1993 (Figure 1). Chlorophyll *a* concentrations were measured since 1971. Physical and chemical measurements of the water and water samples for nutrient concentrations, chlorophyll *a* concentration, and phytoplankton enumeration and identification were collected at 1-meter depth. Phytoplankton cell volumes (μm^3) were calculated from cell dimensions and corrected to account for the large vacuole in diatoms (Strathmann 1967). Details of the analytical methods for physical, chemical, and biological variables are described in Lehman (1996a, 1996b).

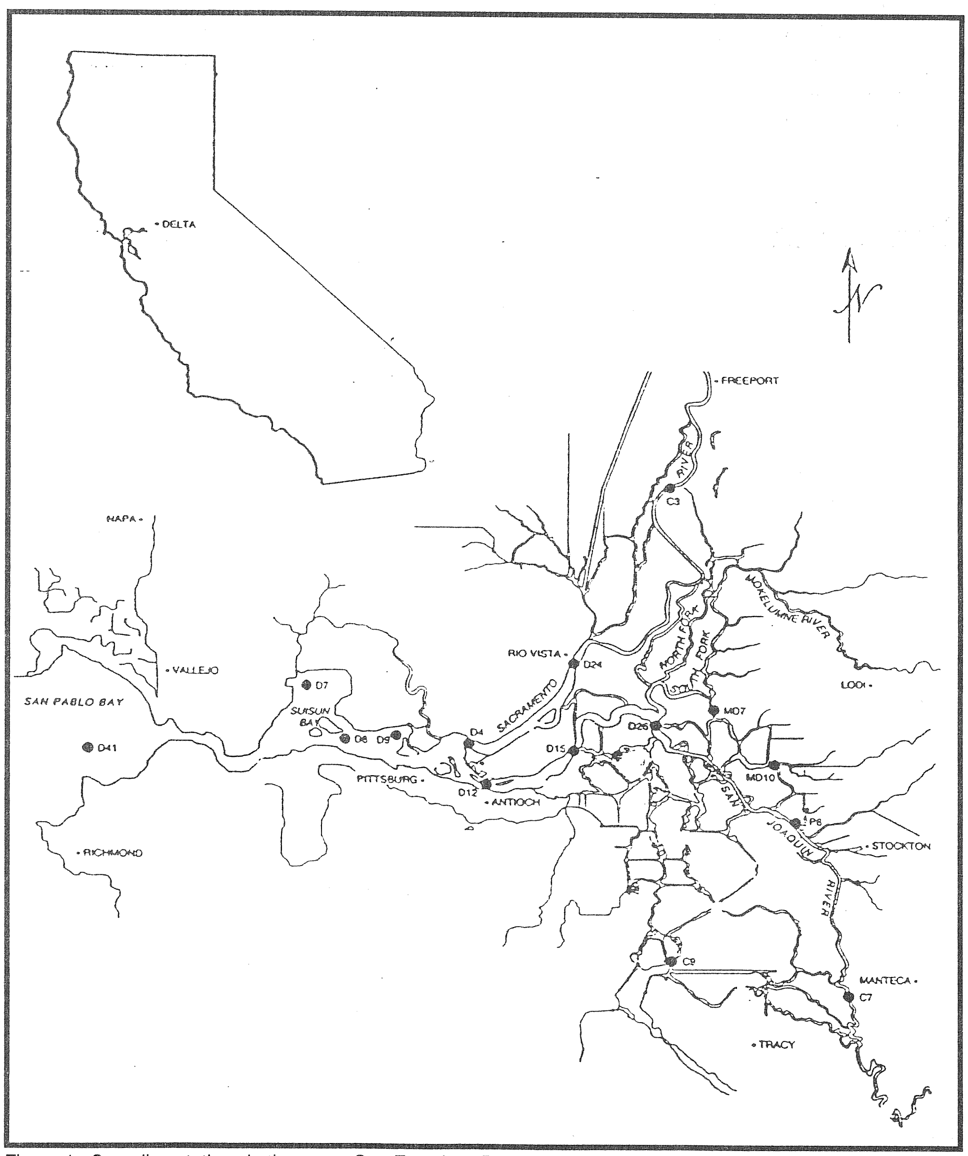

Figure 1 Sampling stations in the upper San Francisco Bay estuary.

Changes in climate were described using the CASLP (California sea level pressure) climate index developed by Dan Cayan. The index is derived from sea level pressure at 40°N and 120°W and separates wet and very dry conditions.

Each year was indexed by water-year type. Water years since 1906 have been classified as wet, above normal, below normal, dry, or critical (very dry) based on the Sacramento River index, which is an estimate of the combined unimpaired runoff of four rivers that flow into the delta. For this study, below- and above-normal years were coded as normal years because only 3 years were in these two water-year types since 1975.

All analyses were conducted with seasonally corrected standard deviation units. These units were calculated for each station and variable as the monthly average minus the average for that month over all years divided by the standard deviation for that month over all years. Only the spring and summer months April through September were used in the analysis.

Differences among environmental and biological variables among water-year types were determined using the nonparametric technique, the Kruskal-Wallis test. Significant differences were at the 0.05 significance level or higher. The conservative nature of a nonparametric statistical technique was used to compensate for the presence of significant correlations by chance alone when a large number of correlations are calculated.

Climatically related environmental change was calculated as the covariance between monthly values of the CASLP climate index and environmental variables at each station among water-year types. This climatically related environmental variation was summarized by four principal component axes. Correlations between the principal component scores of these axes and phytoplankton density or biomass variables were computed with Pearson correlation coefficients.

Phytoplankton Density, Biovolume, and Chlorophyll *a* Concentration

Phytoplankton density, chlorophyll *a* concentration, and biovolume were lower than average for most of the years after 1976. For biovolume and chlorophyll *a* concentration, which are estimates of phytoplankton biomass, 9 to 11 of the 17 years after 1976 were below average (Figure 2). Biovolume and chlorophyll *a* concentration also changed in a similar fashion among years, with values higher than average in the high-outflow years 1982 and 1986. Chlorophyll *a* concentrations measured since 1971 suggest the frequency of lower-than-average values after 1976 is part of a long-term decline. Total density was lower than average for 8 of the years after 1976 and higher than average in 1982. Unlike the other variables, total density was consistently at or slightly above average during the 1987-1992 drought.

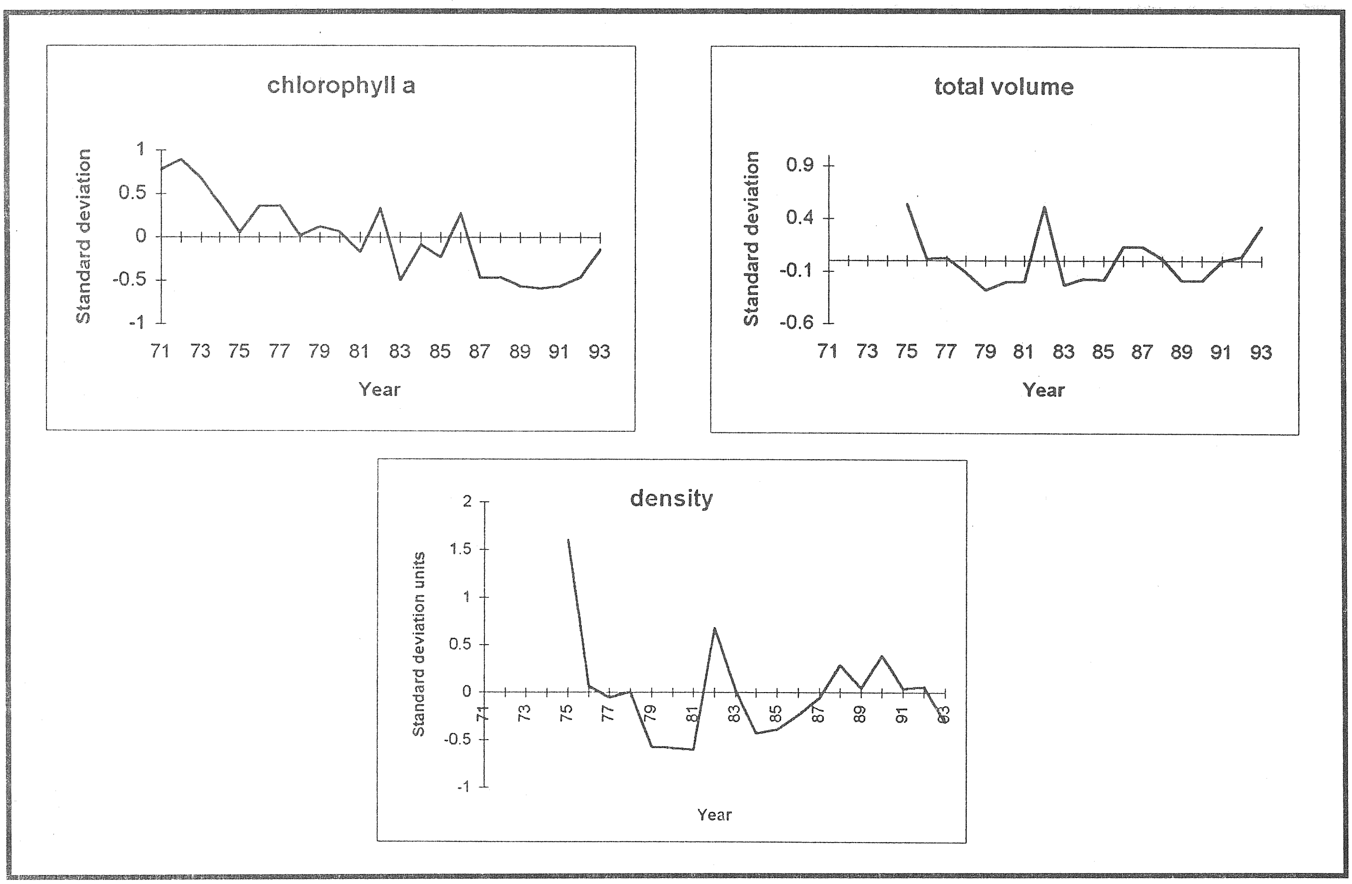

Figure 2 Average standard deviation units for phytoplankton total density, chlorophyll *a* concentration, and biovolume during spring and summer for 15 stations. n=90/year.

Percent Community Composition

The decreased chlorophyll *a* concentration, total density, and biovolume after 1976 were associated with a decrease in the percentage of diatoms in the phytoplankton community. For total density, the percent diatoms decreased from a maximum of about 75% in the late 1970s and early 1980s to a minimum of 30% in 1990 (Figure 3). Percentages increased to near 50% in the early 1990s. For biovolume, the percentage of diatoms decreased from maxima of near 85% in the late 1970s and early 1980s to a minimum of 55% in 1990 before increasing to near maximum values in the early 1990s. The decrease in percent diatoms was accompanied by an increase in greens, bluegreens, and all flagellate groups — cryptophytes, miscellaneous flagellates, dinoflagellates, chrysophytes, and green flagellates. Each of these phytoplankton groups increased by 10-20% in the late 1970s and early 1980s and reached a maximum in the drought period of the late 1980s or 1990.

The decrease in the percentage of diatoms occurred in all regions of the upper estuary. Percent biovolume data suggest the percentage of diatoms among regions was 80-95% in the late 1970s and decreased to as low as 20% in 1990 (Figure 4). The largest decrease was in the northern, lower

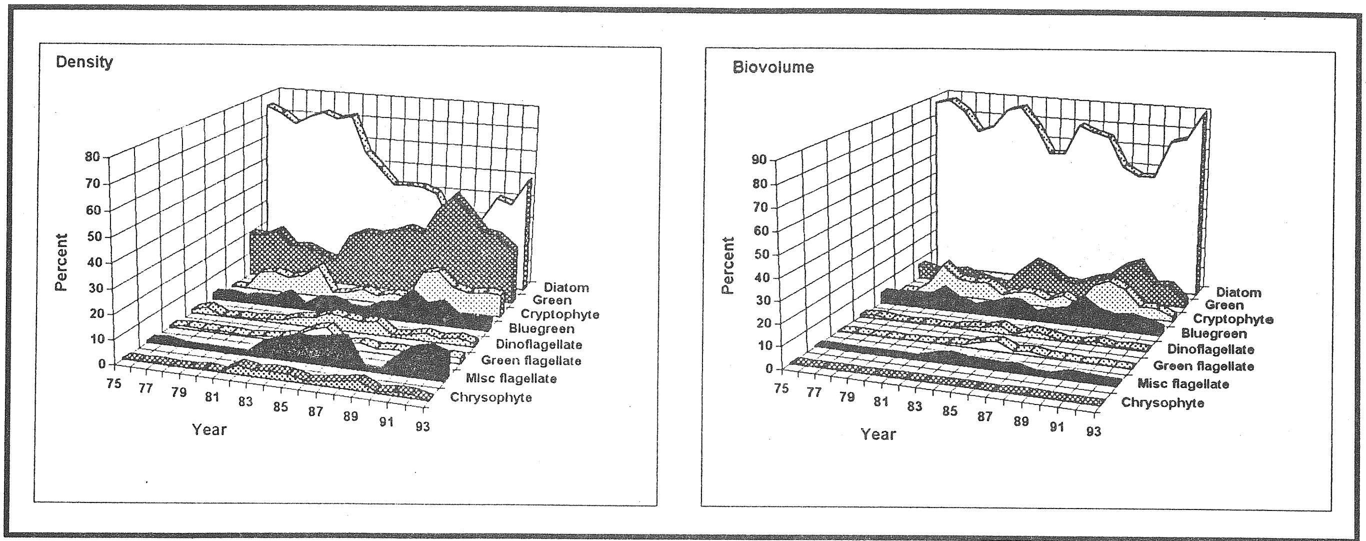

Figure 3 Average percent composition of phytoplankton groups, by density and biovolume.

San Joaquin River, Suisun Bay, and San Pablo Bay regions. For all regions, there was a coincident increase in greens, bluegreens, and flagellates, especially cryptophytes, which each increased to 20-30% of the total biovolume.

Pennate and Centric Diatoms

Among the diatoms, there was a greater loss of pennate than centric biovolume. Average pennate biovolume decreased after 1976 and was consistently lower than average after 1982 (Figure 5). Although biovolume increased consistently after the minimum in 1984, it did not reach above-average values. Average centric biovolume also decreased to below-average values for most years after 1976, reaching a minimum in 1990, but increased to above-average values during the wet years 1982, 1986, 1987, and 1993. Pennate and centric biovolume often varied in an opposite fashion.

The greater loss of pennate than centric diatoms was reflected in percent composition data, with pennate biovolume decreasing to only a few percent of total diatom biovolume in the mid- to late-1980s. Pennate biovolume decreased from a maximum of 35% of the total diatom biovolume in 1978 to less than 5% of the total in 1987 (Figure 6). Although the percentage increased between 1989 and 1990, it decreased again in 1991 to 1993. Percent composition data also demonstrated the strong inverse association between centric and pennate diatom biovolume.

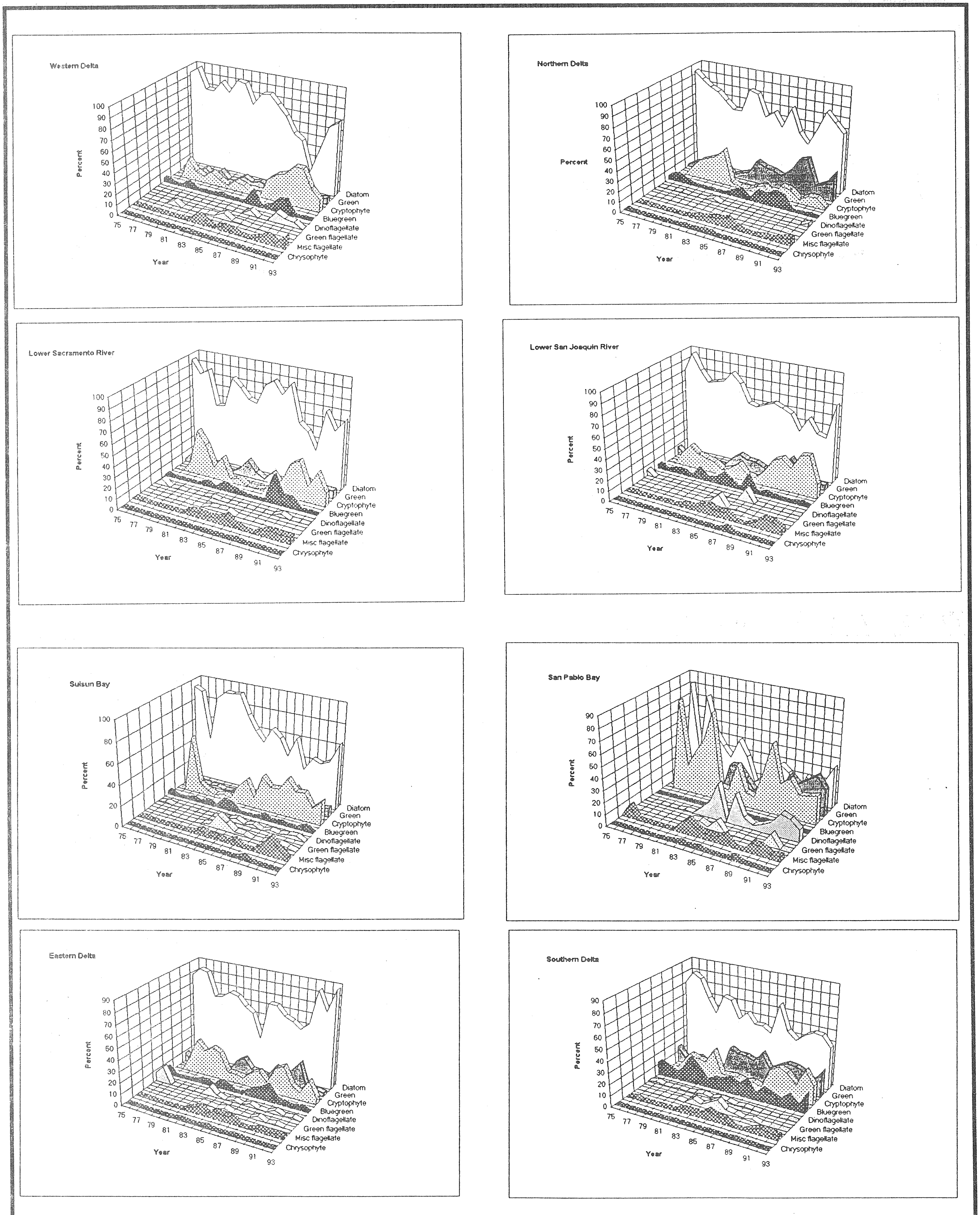

Figure 4 Average percent biovolume of phytoplankton groups among stations in the upper estuary for the spring and summer.

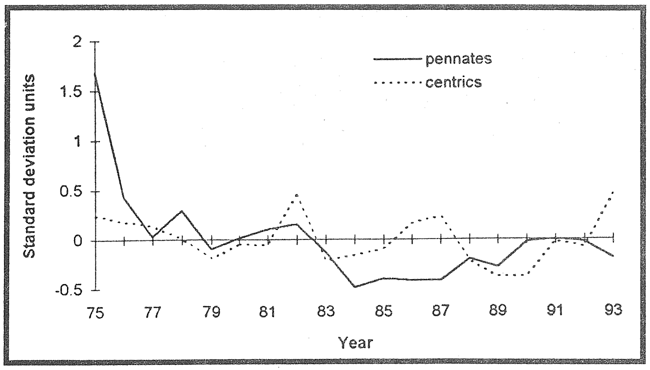

Figure 5 Average standard deviation units for pennate and centric diatoms.

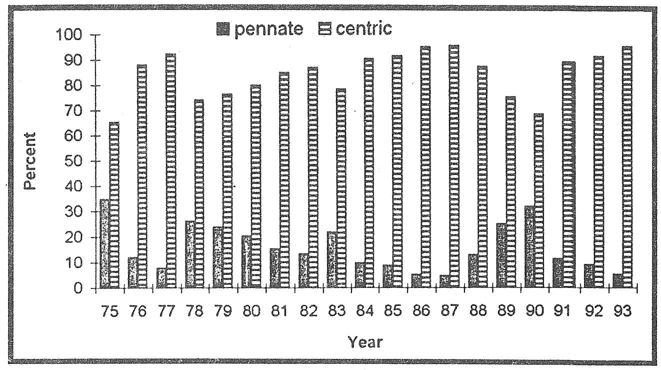

Figure 6 Average percent composition of pennate and centric biovolume.

Changes with Water-Year Type

The climate shift in 1977 increased the frequency of wet and critical water-year types. Dry and critical water-year types comprised 10 of the 19 years 1975-1993 and were accompanied by 7 wet years (Figure 7). This high frequency of dry and critical water-year types is unmatched over the nearly 100 years of record.

Water-year types have significantly different environmental conditions and phytoplankton communities. The nonparametric statistical test, the Kruskal-Wallis test, was used to determine significant ($p<0.05$) differences between water-year types for physical, chemical, and biological variables measured monthly at 15 stations. Nearly all physical and chemical variables were significantly different for the water-year type

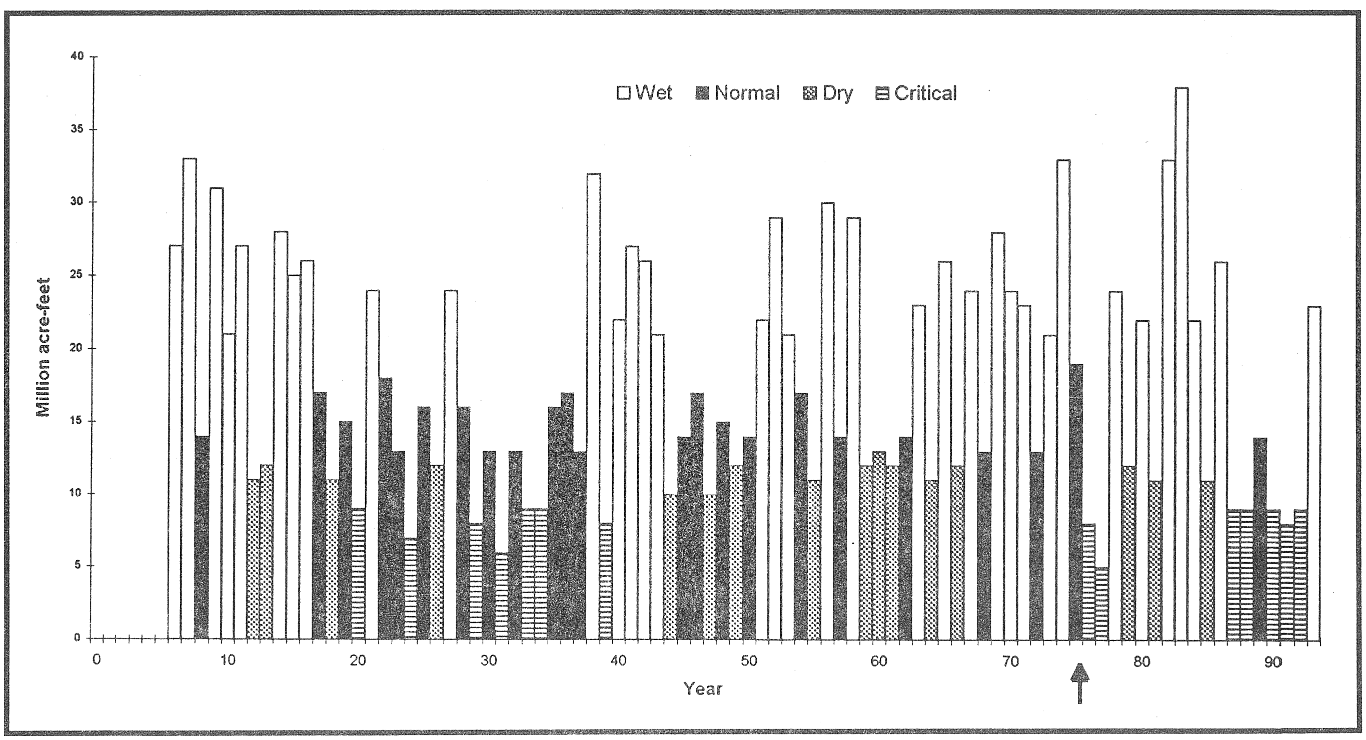

Figure 7 Sacramento Basin unimpaired streamflow, 1906-1993.

comparisons wet/critical, normal/critical, and wet/dry (Table 1). Most differences were also significant for comparisons of water-year types with similar conditions: normal/wet and dry/critical. Differences in environmental conditions among water-year types were matched by those for phytoplankton community composition, with over half of the phytoplankton groups differing for each water-year type comparison.

Table 1
SIGNIFICANT DIFFERENCES IN ENVIRONMENTAL AND BIOLOGICAL VARIABLES AMONG WATER-YEAR TYPES

Significant differences at the p<0.05 level or higher are marked with an X.

	SPRING - SUMMER					
VARIABLE	WET / NORMAL	WET / DRY	WET / CRITICAL	NORMAL / DRY	NORMAL / CRITICAL	DRY / CRITICAL
PHYSICAL						
Air temperature		X	X	X	X	
Secchi disk depth		X	X	X	X	X
Water temperature		X	X	X	X	
Turbidity		X	X	X	X	X
Wind velocity			X		X	X
NUTRIENTS						
Total phosphate		X	X	X	X	X
Silica	X	X	X	X	X	
Organic nitrogen		X	X	X	X	
Ammonia nitrogen	X	X	X	X	X	
Nitrate		X	X		X	X
Ortho-phosphate	X	X	X	X	X	X
CHEMICAL						
Dissolved oxygen		X	X	X	X	
Specific conductance	X	X	X	X	X	X
pH	X	X	X		X	X
Suspended solids		X	X	X	X	X
Total dissolved solids	X	X	X	X	X	X
Volatile solids	X	X	X	X	X	
			X		X	X
STREAM FLOW						
Sacramento River		X	X		X	X
San Joaquin River	X	X	X		X	X
Mokelumne River	X	X	X		X	X
Consumnes River			X			
Miscellaneous flow						
Rio Vista flow		X	X	X	X	X
Outflow	X	X	X	X	X	X
Delta export pumping		X				X
Tracy export pumping					X	
BIOLOGICAL						
Chlorophyll a	X		X		X	X
Diatoms	X	X		X	X	
Greens	X	X	X	X	X	X
Chrysophytes		X		X	X	
Cryptophytes	X		X	X		X
Bluegreens	X	X	X	X	X	X
Dinoflagellates						
Green flagellates	X		X	X		X
Miscellaneous flagellates	X	X			X	X

Environmental Variables

Environmental conditions differed among water-year types. Critical years were characterized by higher-than-average air and water temperature, wind velocity, specific conductance, pH, water transparency, and nutrient concentrations but lower-than-average streamflow and export (Figure 8). All of these conditions were opposite to those in wet years, except for exports, which were also lower than average. Environmental conditions during normal and dry years were a mixture of those for critical and wet years. Normal years, like wet years, had lower-than-average air and water temperature, specific conductance, wind velocity, and nitrate and orthophosphate concentration. Normal years differed from wet years in having higher-than-average water transparency, pH, and silica concentration. Precipitation and outflow were lower than for wet years, but exports were higher. Dry years were similar to critical years except for lower-than-average nitrate concentrations, turbidity, and suspended solids. Dry years also had higher-than-average exports compared with lower-than-average exports during critical years.

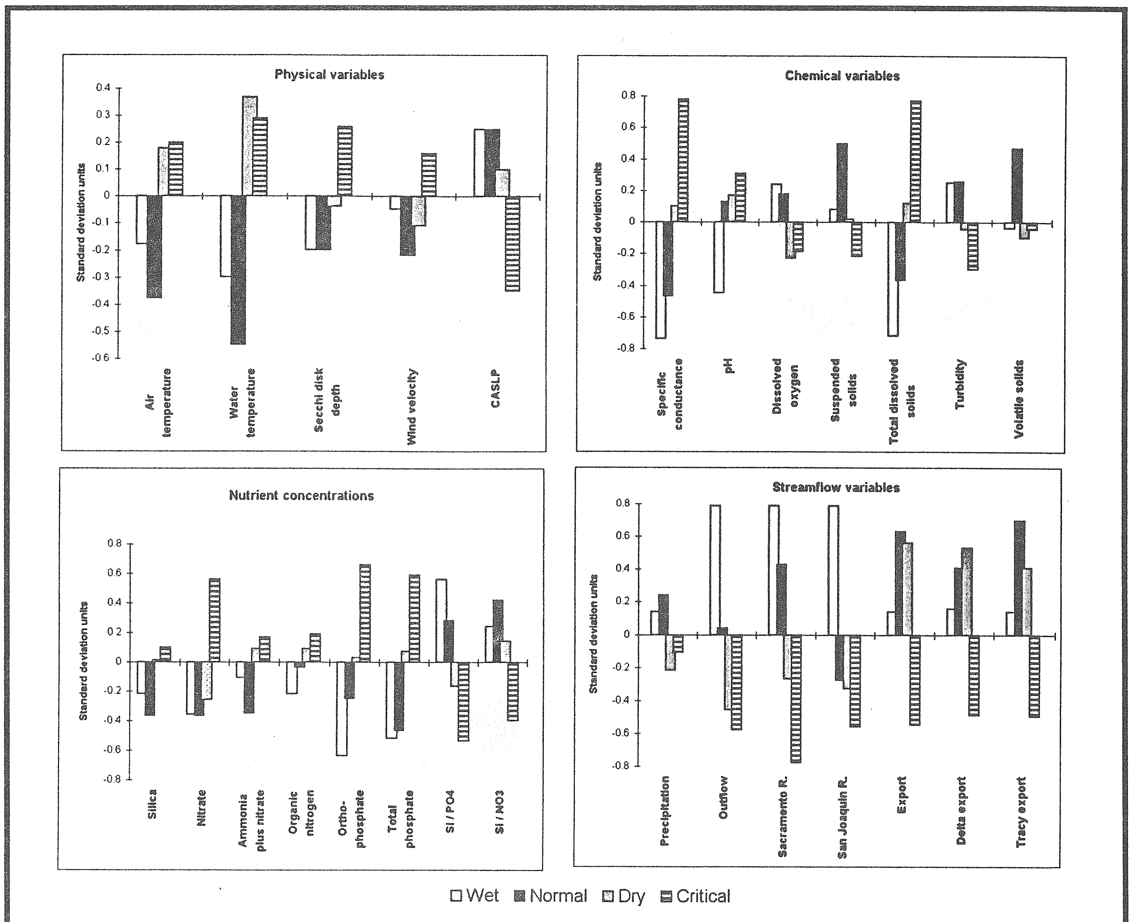

Figure 8 Average standard deviation units for environmental variables among water-year types.

Chlorophyll *a* Concentration, Biovolume, and Total Density

The largest differences in chlorophyll *a* concentration, biovolume and total density occurred between wetter versus drier water-year types. Average chlorophyll *a* concentration, phytoplankton biovolume, and total density were well above average during wet and normal years but only slightly above average during critical years (Figure 9). The poorest phytoplankton growth was probably during dry years, when total density and biovolume were well below average.

Community Composition

Changes in chlorophyll *a* concentration, biovolume, and total density among water-year types were associated with a shift in community composition. Biovolume and total density (not shown) of diatoms, greens, and bluegreens were higher during wet and normal years; flagellate groups (cryptophytes, dinoflagellates, green flagellates, and miscellaneous flagellates) were higher during dry and critical years (Figure 10). In addition, some phytoplankton groups increased in opposite water-year types; miscellaneous flagellates increased in critical/dry and wet years, and greens increased in normal and critical years.

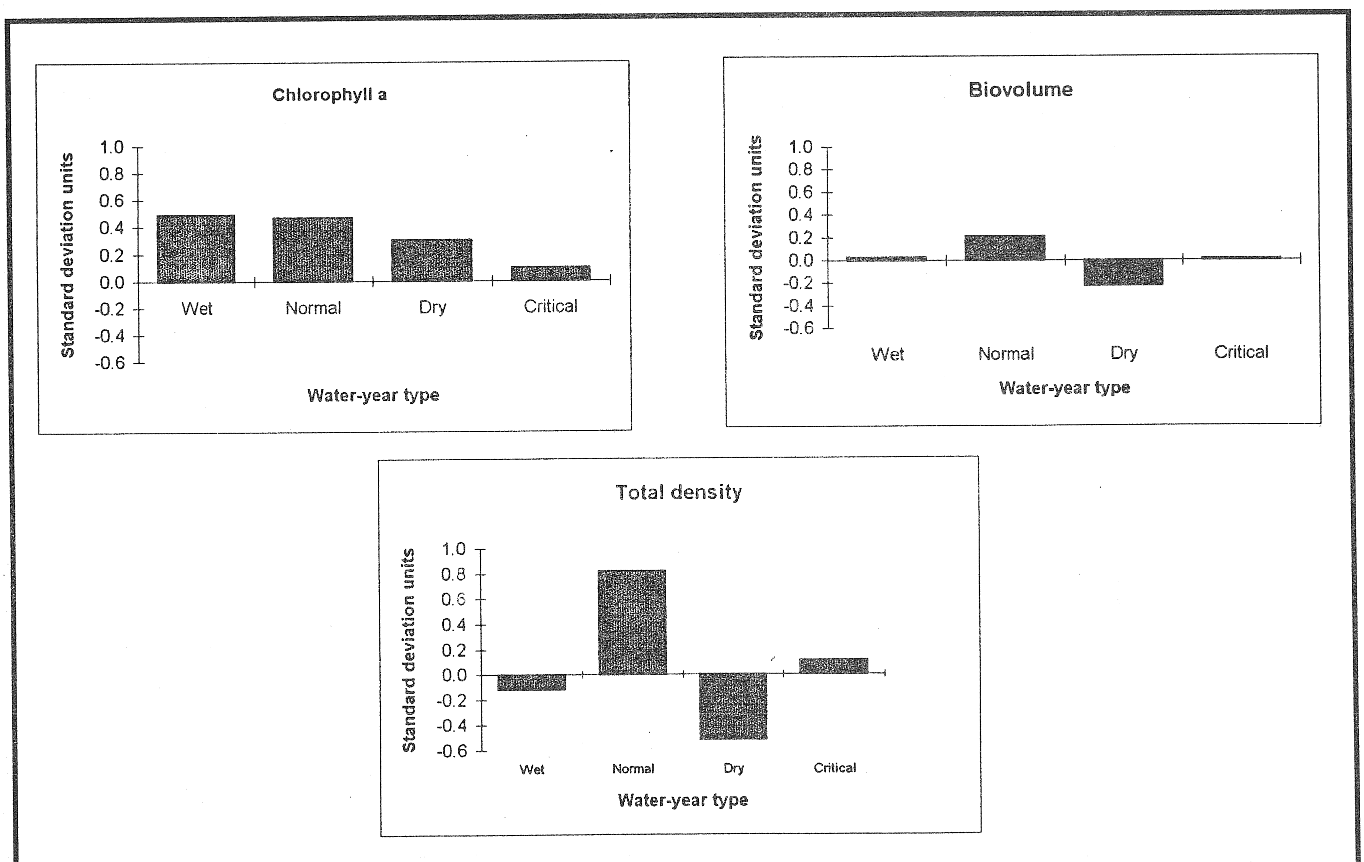

Figure 9 Average standard deviation units for chlorophyll a concentration, biovolume, and total density among water-year types.

Pennate and Centric Diatoms

Among the diatoms, biovolume and density (not shown) were higher for pennate and centric diatoms during wet and normal years (Figure 11). However, biovolume and density of these two types of diatoms differed for drier years, with centrics being more abundant or having higher biovolume during dry and critical years. The direction of change for these diatom groups among water-year types persisted at the species level. Normal and wet years had more pennate diatoms; wet years and dry or critical years had more centric diatoms (Figure 12).

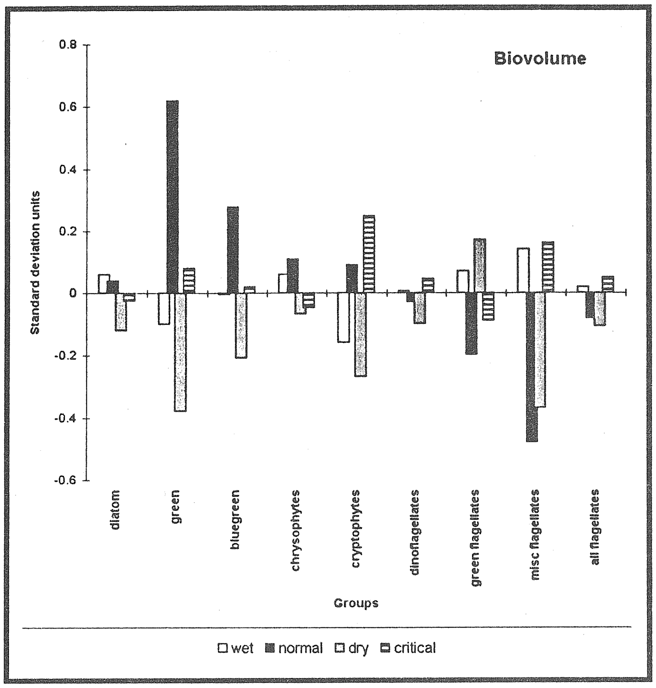

Figure 10 Average standard deviation units for biovolume of phytoplankton groups among water-year types.

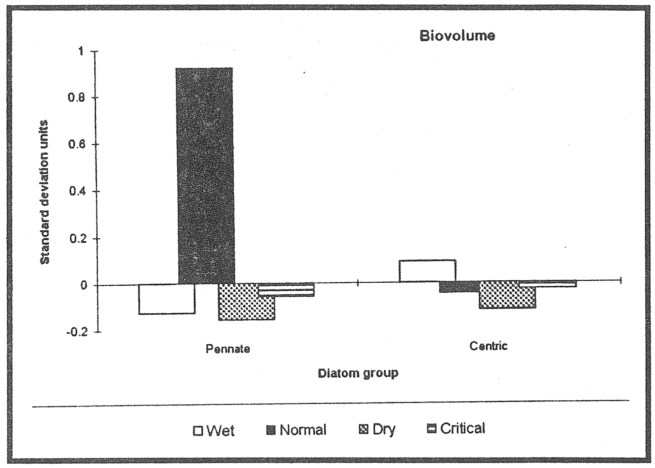

Figure 11 Average standard deviation units for biovolume of pennate and centric diatoms among water-year types.

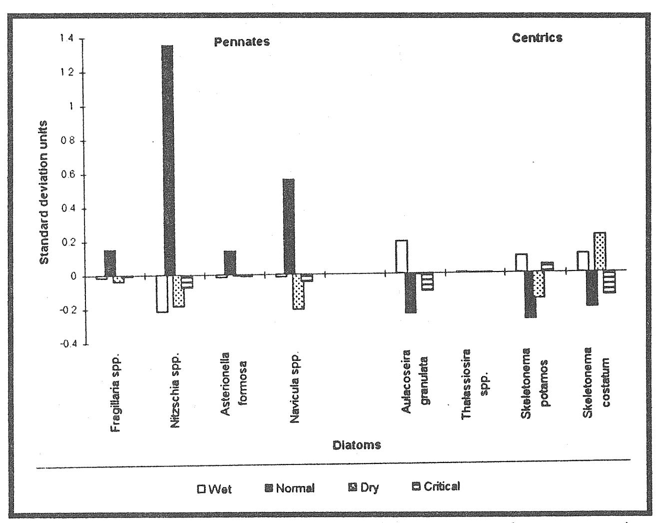

Figure 12 Average standard deviation units for biovolume of pennate and centric diatom species among water-year types.

Associations between Climate-Related Environmental Variables and Phytoplankton Biomass and Community Composition

Principal component analysis was computed from a station by water-year type covariance matrix developed for the CASLP climate index and a suite of environmental variables. Uncorrelated (r <0.70) variables within the covariance matrix were summarized by three axes using principal component analysis (Table 2). Together these axes described 69% of the environmental variation. Most of the climate-related environmental variation was associated with Axis 1, which described conditions associated with very dry conditions: high water temperature, water transparency, specific conductance, wind velocity, nutrient concentrations,and export but low outflow. Axis 2 described dry conditions with low silica and high wind, while Axis 4 described conditions of average flow, high water temperature and low specific conductance.

Table 2
PRINCIPAL COMPONENT ANALYSIS COMPUTED FOR CLIMATICALLY RELATED ENVIRONMENTAL VARIABLES

	Principal Component Axes		
Variable	**Axis 1**	**Axis 2**	**Axis 3**
Outflow	-0.44	-0.31	-0.03
Export	0.39	0.01	-0.30
Secchi disk depth	0.29	0.35	0.29
Water temperature	0.27	-0.07	0.42
Wind	0.13	0.45	0.21
Specific conductance	0.22	0.34	-0.48
pH	-0.40	0.15	-0.07
Dissolved oxygen	-0.27	0.39	0.47
Nitrate	0.37	-0.19	-0.01
Silica	0.24	-0.50	0.37
Percent variation	**38**	**17**	**14**

Correlations between principal component axes scores and phytoplankton variables were often highly significant for Axis 1. The very dry environmental conditions described by Axis 1 were negatively correlated with total biovolume and total density but not chlorophyll *a* concentration (Table 3). Among phytoplankton groups, correlations with Axis 1 and biovolume or density were negative for diatoms, greens, and bluegreens but positive for green and miscellaneous flagellates. Among the diatoms, Axis 1 was negatively (biovolume) or more negatively (density) correlated with pennates than centrics.

Correlations between the other principal component axes and phytoplankton variables were less consistent than for Axis 1. Correlations with Axis 2 were negative for most of the diatoms and total density or biovolume, but positively or not significantly correlated with flagellates, which do not require silica. Correlations with Axis 3 were negative for centric diatoms and flagellates, which are common when specific conductance is high in the delta.

Correlations between environmental axes and phytoplankton groups persisted at the species level (Table 4) and provided more information on variation within each group. Positive correlations with the dry conditions of Axis 1 and centric diatoms were primarily associated with chain-forming species. Cryptophytes increased when specific conductance was high, but not the common form, *Rhodomonas lacustrus*. *Skeletonema costatum* increased with dry and warm conditions, but not if silica was low. Green species decreased with dry and warm conditions, but not the flagellated species *Carteria* spp.

Table 3
CORRELATIONS BETWEEN
PRINCIPAL COMPONENT AXES SCORES AND
PHYTOPLANKTON GROUP DENSITY AND BIOMASS

n=60

Biovolume

Variables	Principal component axes Axis 1	 Axis 2	 Axis 3
Chlorophyll a		-0.26	
Total volume	**-0.35**	-0.29	
Diatom - all		-0.31	
centric			
pennate	**-0.80**	-0.34	
Green	**-0.65**	-0.27	-0.29
Chrysophyte			
Cryptophyte			**-0.42**
Bluegreen	**-0.60**		-0.31
Dinoflagellate			
Green flagellate	**0.46**		
Misc flagellate	**0.43**		**-0.47**

Density

Variables	Principal Component Axes Axis 1	 Axis 2	 Axis 3
Total density	**-0.74**	-0.30	-0.26
Diatom - all	**-0.74**	**-0.35**	
centric	-0.30	-0.30	-0.27
pennate	**-0.81**	**-0.33**	
Green	**-0.71**	0.30	
Chrysophyte			
Cryptophyte	**-0.50**	0.29	**-0.37**
Bluegreen	-0.50		-0.33
Dinoflagellate			-0.28
Green flagellate	**0.40**		
Misc flagellate	**0.45**		**-0.46**

significance is at the .01 (bold type) or .05 (regular type) level

Table 4
CORRELATIONS BETWEEN
PRINCIPAL COMPONENT AXES SCORES AND
PHYTOPLANKTON SPECIES BIOVOLUME

n=60

Biovolume	Species	Principal Component Axes Axis 1	 Axis 2	 Axis 3
Diatom - centric	Aulacoseira granulata	**0.48**		
	Skeletonema costatum	**0.37**	**-0.34**	0.32
	Skeletonema potamos	0.31		**-0.36**
	Thalassiosira spp.			
	Cyclotella spp.	**-0.54**	-0.27	
	Stephanodiscus spp.	**-0.64**	-0.32	
Diatom - pennate	Asterionella formosa	**-0.66**		
	Nitzschia spp.	**-0.79**	-0.33	
	Achnanthes spp.	**-0.64**	0.27	
	Gomponema spp.	**-0.45**		
	Tabellaria fenestra			-0.29
	Cymbella spp.	**-0.63**		
	Rhoicosphenia spp.	**-0.66**		
	Fragilaria spp.	**-0.43**		
Green	Carteria spp.	0.29		-0.35
	Chlamydomonas spp.	**-0.80**	**-0.34**	
	Pediastrum spp.	**-0.44**		
Chrysophyte	Chroomonas spp.			
Cryptophyte	Rhodomonas lacustrus	**-0.66**		
Bluegreen	Anacystis spp.	**-0.70**		
	Anabaena spp.		**-0.34**	
Dinoflagellate	Gymnodinium spp.			
Green flagellate	Euglena spp.			
	Phacus spp.	**0.53**		0.28
Misc flagellate		**0.45**		**-0.46**

Significance is at the <0.01 level (bold type) or <0.05 level (regular type).

Discussion

Climate-related changes in environmental conditions were significantly correlated with long-term changes in phytoplankton density, biovolume, and chlorophyll *a* concentration among water-year types. These findings support previous studies that demonstrated that interannual changes in phytoplankton community composition and chlorophyll *a* concentration since 1976 were correlated with or coincided with changes in environmental factors influenced by climate (Lehman and Smith 1991; Lehman 1992). The current study suggests this interannual variability is strongly linked to dry and critical water-year types after 1976. Climate has a major effect on precipitation and streamflow in California (Cayan and Peterson 1989). Many of the climate effects on phytoplankton are probably a function of streamflow, which affects nutrient concentrations, salinity, turbidity, and residence time in San Francisco Bay (Conomos 1979; Cloern *et al* 1983; Peterson *et al* 1986, 1989).

Mechanisms by which dry climatic conditions may have influenced the loss of diatoms and shift in the centric/pennate ratio are suggested by phytoplankton physiology and ecology. Diatoms are generally more abundant during the spring, when water temperature is cool and wind and turbidity are high, and decrease in the summer, when conditions are dry, like the climatic conditions after 1976. In the delta, however, some chain-forming centric diatoms — *Skeletonema potamos*, *Aulacoseira granulata,* and *Thalassiosira spp.* — bloom in the lower San Joaquin River during the summer, when water temperature and salinity are high. These centric diatoms contrast with pennate diatoms, which often characterize cold freshwater habitats (Kingston *et al* 1983), and may partly explain the larger negative correlation between dry conditions and pennate diatoms than centric diatoms. Single-celled diatoms in the upper estuary are also large cells (Lehman 1996a) with rapid settling rates (Ball 1981) that rely on vertical mixing to maintain position in the euphotic zone. During dry conditions, high residence times promote the settling of diatoms to the bottom, where they also become susceptible to grazing by benthos (Nichols 1985). The stable water column in the summer, however, may also promote blooms of chain-forming diatoms, which have increased buoyancy because of their large surface area. Some diatoms may also respond negatively to the increased water transparency during very dry conditions, because they usually occur in turbid environments where high accessory pigment content provides a competitive advantage. Lastly, reduced nutrient loading during dry conditions affects nutrient ratios, which affect diatom abundance and community composition, even when nutrients are in excess (Sommer 1994; Kilham *et al* 1996).

The potential for climate to influence diatom density and biomass is an important factor for the estuarine food web. Large single-celled diatoms have a high cellular carbon content (Lehman 196a) and are a common food of large zooplankton, like *Neomysis mercedis* (Kost and Knight 1975). In fact, adult zooplankton select for large cells. Adult zooplankton grazing and ingestion are higher when phytoplankton cell diameter is larger than 8 to 11 µm (Paffenhoffer and Knowles 1978; Peterson *et al* 1991; Kiorboe *et al* 1990) and is a function of the linear size ratio between predator and prey (Hansen *et al* 1994). Absence of large-diameter cells can lead to intra- and inter-species competition for food quantity (Paffenhoffer 1971; Paffenhoffer and Knowles 1978) and quality (Peterson *et al* 1991). The importance of the greater loss of pennate than centric diatoms to the food web is unclear, because the utility of chain-forming centric diatoms as food varies (Paffenhofer 1971; Gliwicz 1980). Most of the blooms in the delta are long-chain-forming centric diatoms, including *Aulacoseira granulata*, but grazing is low when chains are long (Fulton 1988).

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